Oviposition Behavior and Egg Parasitoids of *Sophonia rufofascia* (Homoptera: Cicadellidae) in Hawaii Volcanoes National Park

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Abstract. Oviposition behavior of *Sophonia rufofascia*, a polyphagous leafhopper recently introduced to the Hawaiian Islands, was studied on 6 common plant hosts in Hawaii Volcanoes National Park. The average number of eggs per leaf was approximately 1 in ’a’ali’i (*Dodonea viscosa*) and firetree (*Myrica faya*), and closer to 2 in Hawaiian holly (*Ilex anomala*), ’ohi’a lehua (*Metrosideros polymorpha*), sandalwood (*Santalum paniculatum*) and ’ohelo (*Vaccinium calycimum*). Over all plant species there was a weak positive correlation between leaf size and the number of eggs. All oviposition scars were in the midvein of ’a’ali’i, firetree, ’ohi’a lehua, and ’ohelo, but in holly and sandalwood oviposition also occurred away from the midvein. In holly, the proportion of eggs laid away from the midvein was positively correlated with leaf thickness. Variation among host plants also existed for egg position relative to the basal, middle, and apical third of the leaf, but in all species the middle third of the leaf was the most common oviposition site. *S. rufofascia* eggs in the park are attacked principally by two endemic mymarids in the genus *Polynema*; this represents a host shift or host range expansion for these native wasps.

Introduction

The two-spotted leafhopper, *Sophonia rufofascia* (Kuoh and Kuoh) (Homoptera: Cicadellidae) is a recent accidental introduction into the Hawaiian Islands. It was first discovered on the island of Oahu in 1987 (Kumashiro and Heu 1989) and has since spread to all the major islands in the archipelago. *S. rufofascia* has been recorded from 307 species of plants in 83 families, of which 66 are endemic or indigenous to the Hawaiian Islands and 15 are on the federal list of endangered species in the U.S. (Fukada 1996). On most hosts, feeding by *S. rufofascia* results in interveinal chlorosis or leaf distortion, but in a few hosts, plant death can occur. Damage can also occur when females deposit eggs in the leaf midvein, which blocks vascular tissue. Several plants in Hawaiian forests and watersheds are particularly susceptible to *S. rufofascia* feeding. For example, leafhopper feeding has been implicated in the dieback of large patches of the native false staghorn fern, *Dicranopteris linearis,* a dominant understory and gap species in Hawaiian forests and watersheds; dead uluhe patches often do not regenerate and become overrun by exotic weeds (Follett and Jones unpublished).

In Hawaii Volcanoes National Park (HAVO) on the island of Hawaii, *S. rufofascia* is attacking several important tree species. Large areas of dieoff of *Metrosideros polymorpha* (’ohi’a lehua), the dominant tree in the native Hawaiian forest, have been linked to increased levels of leafhopper activity. Ironically, the other key species suffering from *S.*

rufofascia feeding is *Myrica faya* (firetree), a weedy shrub that itself has radically changed the structure of the forest community in HAVO (Vitousek et al. 1987). The threat posed by *S. rufofascia* to native Hawaiian forest communities has stimulated research on the ecology and behavior of *S. rufofascia*. Because the principal natural enemies of *S. rufofascia* are egg parasitoids, we have been interested in the leafhopper's oviposition behavior relative to different plant hosts.

Oviposition behavior has been studied in several groups of leafhoppers (Claridge and Reynolds 1972, Claridge et al. 1977, Thompson 1978, Stiling 1980, Heady et al. 1985). All the leafhopper species in these studies were host plant-specific, and demonstrated species-specific oviposition behavior. For example, among 7 species of *Dalbulus* leafhoppers on maize, *D. quinquenotatus* and *D. maidis* clustered their eggs while the other 5 species did not; *D. gelbus* and *D. tripsacoides* laid a significant portion of their eggs off the midrib while the other 5 did not; and so forth. Studies examining oviposition patterns in polyphagous leafhoppers across hosts are rare and virtually nothing is known about the natural history of *S. rufofascia*, in Hawaii or elsewhere. Here we report differences in oviposition behavior in *S. rufofascia* on 6 different host plants. We also report on several species of egg parasitoids attacking *S. rufofascia* on these host plants in the park.

Materials and Methods

Approximately 100 leaves containing *S. rufofascia* oviposition scars were collected from each of 6 host plants in Hawaii Volcanoes National Park, and brought into the laboratory for examination under a dissecting microscope. Backlighting under the scope silhouettes the egg chamber, and in our experience visible oviposition scars invariably contain eggs. The 6 hosts were firetree (*Myrica faya*), 'a'ali'i (*Dodonaea viscosa*), sandalwood (*Santalum paniculatum)*, 'ohi'a lehua (*Metrosideros polymorpha*), Hawaiian holly or kawa'u (*Ilex anomala)*, and 'ohelo (*Vaccinium calycinum*). Hawaiian holly, 'ohelo, 'ohi'a lehua, and sandalwood are all endemic to Hawaii, while 'a'ali'i is indigenous. Firetree was introduced from the Azores and Madeira around 1900 and has been in HAVO since the early 1960s (Whiteaker and Gardner 1992). 'A'ali'i and 'ohi'a lehua leaves were collected from Hilina Pali Rd. at 1000 m elevation where the average annual rainfall is 1270 mm, and sandalwood, holly, and 'ohelo leaves were collected from Crater Rim Dr. at an elevation of 1140 m where the average rainfall is 2540 mm. For each leaf, data were taken on leaf dimensions (length of blade, width at center), leaf thickness (at midpoint of midrib), total number of oviposition scars, whether the scar was on the midrib or off the midrib, position of the scar relative to the basal, middle or apical third of the leaf, and the diameter of the midrib at the oviposition scar (when appropriate). When an egg could be extracted intact, measurements were made of its length and width using an ocular micrometer. Data across plant species on the total number of oviposition scars, proportion of eggs laid in the midrib, proportion of eggs in the basal/middle/apical portions of the leaf, and vein diameter were subjected to analysis of variance and Tukey-Kramer's HSD ($\partial = 0.05$) was used to make paired comparisons among means for the 6 plant species (JMP 3.1.5, SAS Institute 1994). Pairwise correlations were made for total eggs laid, proportion of eggs laid in the midvein, leaf thickness, leaf area by calculating Pearson product-moment correlation coefficients (JMP 3.1.5, SAS Institute 1994).

For each plant species, a minimum of 100 leaves with leafhopper oviposition scars was collected and held in plastic bags for parasitoid emergence. Other homopterans, including native *Nesophrosyne* leafhoppers and delphacid planthoppers, also occur in HAVO and lay eggs in leaves (Zimmerman 1948). However, in a preliminary study, numerous leaves bearing oviposition scars from each of our 6 host plants in the park were held for emergence and

Table 1. Measurements of leaves with *S. rufofascia* oviposition scars for six tree species.

Species	n	Length (mm)	Width) (mm)	Leaf area (cm^2)[z]	Leaf thickness (mm)
			Mean ± SE		
’a’ali’i	48	39.4 (1.0)	13.1 (0.4)	4.2 (0.2)	0.68 (0.12)
holly	48	50.5 (0.9)	32.5 (0.6)	13.1 (0.5)	0.86 (0.35)
firetree	48	28.3 (0.8)	9.0 (0.3)	2.0 (0.1)	0.59 (0.13)
’ohi’a lehua	48	30.5 (0.7)	19.1 (0.5)	4.6 (0.2)	0.59 (0.15)
sandalwood	48	50.0 (1.1)	36.1 (0.9)	14.4 (0.6)	0.69 (0.23)
’ohelo	48	61.0 (1.5)	26.8 (0.9)	13.2 (0.8)	0.70 (0.19)

[z]leaf area (ellipse) = πab, where a = length/2 and b = width/2

no homopteran species other than *S. rufofascia* was ever recovered. This indicates *S. rufofascia* is probably responsible for the vast majority of oviposition scars in these plants. Also, while inspecting plants and collecting leaves from the 6 host plants over the course of this study other auchenorrynchous Homoptera were seldom observed. Therefore, we assume that parasitoids emerging from our leaf samples, and known to attack leafhopper eggs (Huber 1986), developed from *S. rufofascia* eggs. All leafhopper parasitoids and other incidental parasitoids emerging from our leaf samples were identified by Dr. John Huber (Canadian Forest Service, Ottawa).

Results and Discussion

The leaves of the 6 host plants varied in their gross morphology (Table 1). Holly, sandalwood and ’ohelo leaves were generally larger than the leaves from ’ohi’a lehua and ’a’ali’i. ’A’ali’i and firetree have slender leaves compared to the other three species: the length-to-width ratio is approximately 3:1 in ’a’ali’i and firetree, whereas it is about 2:1 or less in sandalwood, ’ohi’a lehua, ’ohelo and holly. Holly has the thickest leaves of the group (Table 1). In general, the leaves of the 6 plant species used for our study were glabrous, which facilitated the search for oviposition scars. ’Ohi’a lehua has both glabrous and pubescent forms, but scars on pubescent leaves are difficult to discern.

All *S. rufofascia* oviposition scars observed in our study indicated that eggs are laid singly. Fourteen eggs were excavated intact from oviposition scars and measured. Egg dimensions averaged 0.32 mm in width (range 0.3–0.35) and 1.34 mm in length (range 1.3–1.4). The number of oviposition scars on the different hosts varied: the average number of eggs per leaf was approximately 1 in ’a’ali’i and firetree with 91% and 97% of leaves having only one scar, respectively, and closer to 2 in holly, ’ohi’a lehua, sandalwood, and ’ohelo (Table 2). The maximum number of oviposition scars in any one leaf was 3 in ’a’ali’i and firetree and reached as high as 9 in ’ohi’a lehua. Over all plant species, there was a slight positive correlation between leaf size and the number of eggs ($r = 0.24$, $n = 288$, $P<0.01$). In holly, the average number of eggs per leaf was not correlated with leaf thickness ($r = 0.08$, $n = 48$, $P = 0.57$), but the proportion of eggs laid in the midvein was negatively correlated with leaf thickness ($r = -0.46$, $n = 48$, $P<0.001$).

Sophonia rufofascia eggs are laid predominantly in the midvein of the leaf; all the oviposition scars observed in ’a’ali’i, firetree, ’ohi’a lehua, and ’ohelo were along the midvein.

Table 2. Number of eggs laid in the leaf by *S. rufofascia*, percent eggs laid in the midvein, and the diameter of the vein at the oviposition site (means ± SE).

Species	n	No. eggs in leaf[z]	Max. no. eggs	% in midvein	n	Vein diam. (mm)	Range
’a’ali’i	78	1.1 (0.05) a	3	100 (0.) a	35	0.68 (0.02) a	0.5–1.0
holly	78	2.2 (0.15) b	6	69.2 (0.04) b	47	0.86 (0.05) b	0.5–2.0
firetree	78	1.0 (0.02) a	3	100 (0.) a	33	0.59 (0.02) a	0.4–1.2
’ohi’a lehua[y]	77	2.0 (0.18) b	9	100 (0.) a	61	0.59 (0.01) a	0.4–0.9
sandalwood	80	1.9 (0.15) b	7	93.5 (0.02) a	14	0.69 (0.06) a	0.4–1.1
’ohelo	78	1.7 (0.12) b	5	100 (0.) a	55	0.70 (0.03) a	0.4–1.0

[z]Means within columns followed by the same letter are not statistically different at $P \leq 0.05$.
[y]Glabrous leaves, only

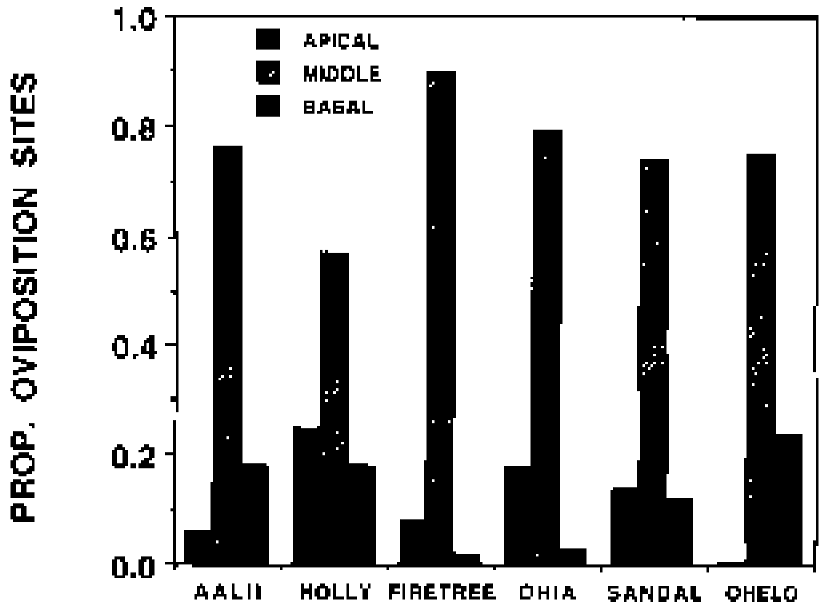
The frequency of oviposition off the midvein was highest in holly (30.8 %), and sandalwood also had scars away from the midvein (6.5%). The prevalence of oviposition away from the midvein in holly may result because the interveinal areas of holly leaves are thicker than those of the other plants we tested (Table 1) and thus allows eggs to be concealed. For the plant species we tested, almost all eggs were laid lengthwise in the vein. Measurements of vein thickness at the site of the oviposition scar indicated that veins were always >0.4 mm in diameter and therefore could completely conceal an egg. Three times in sandalwood we observed eggs deposited perpendicularly to, and half embedded in, the midvein.

Sophonia rufofascia oviposition behavior on the 6 host plants also varied relative to the position along the axis of the leaf where eggs were deposited (Figure 1). The majority of oviposition scars were found in the middle third of the leaf for all plant species. A substantial proportion of scars was found in the basal third of the leaf in ’a’ali’i, holly, sandalwood and ’ohelo, while almost none of the scars on firetree or ’ohi’a lehua were basal. In holly, ’ohi’a lehua and sandalwood, a substantial proportion of egg laying occurred on the apical third of the plant, but this was very rare in ’ohelo. Oviposition site choice may be a function of midvein diameter, midvein toughness or pubescence, or other factors.

Leafhoppers are typically attacked by egg parasitoids, especially parasitoids in the Mymaridae. The endemic mymarid fauna in Hawaii contains about 13 valid, described species in the cosmopolitan genus *Polynema* and probably more than 20 additional endemics (J. Beardsley personal communication). An additional 21 non-endemic species in 10 genera also occur. Two endemic *Polynema* spp. were the most common parasitoids, and 2 other mymarid species, *Schizophragma bicolor* and *Stethynium* sp., were occasionally found, along with a single specimen of a third *Polynema* sp. believed to be endemic. Attack of *Sophonia rufofascia* by the 3 endemic *Polynema* spp. represents a host shift or host range expansion for these wasps, however their native hosts are unknown. Other parasitoids reared from our leaf samples but not attacking *S. rufofascia* were *Megaphragma* sp., a trichogrammatid that attacks thrips eggs; *Alaptus* sp., an adventive mymarid parasitoid of psocid eggs; and *Metaphycus* sp. a encyrtid parasitoid of coccids.

Future studies might focus on oviposition patterns at other sites in the islands; on rates of parasitism of *S. rufofascia* eggs on the different hosts; and on patterns of parasitism relative to oviposition site on a host.

Figure 1. Proportion of *S. rufofascia* oviposition scars located on the apical, middle, and basal third of the leaves from each of the six host plants.



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